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Three New Species of *Leptolalax* from Thailand (Amphibia, Anura, Megophryidae)

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Three new megophryid species, *Leptolalax melanoleucus*, *L. fuliginosus*, and *L. solus*, are described from southwestern and southern Thailand on the bases of acoustic and morphological characteristics. *Leptolalax melanoleucus* and *L. fuliginosus* are similar to *L. pelodytoides* from northern Thailand, but differ from it completely in advertisement call characteristics and ventral color. *Leptolalax solus* is similar to *L. heteropus* from peninsular Malaysia, but differs from it by advertisement call, as well as by some body proportions. The distributional pattern of *Leptolalax* within Thailand is discussed.

Key words: acoustics, *Leptolalax*, new species, Southeast Asia, taxonomy, zoogeography

INTRODUCTION

The number of known species in the Southeast Asian megophryid genus *Leptolalax* has rapidly increased in the last three decades (Dubois, 1983, 1987; Fei *et al.*, 1991; Fei and Ye, 1992; Malkmus, 1992; Matsui, 1997; Inger *et al.*, 1997, 1999; Lathrop *et al.*, 1998; Ohler *et al.*, 2000; Grismer *et al.*, 2004). Analyses of call characteristics, recently added to traditional morphological methods in conducting taxonomic studies on frogs, played an important role in detecting some cryptic members in this genus (Malkmus and Riede, 1993; Matsui, 1997).

Two species of *Leptolalax*, *L. pelodytoides* (Boulenger, 1893) and *L. minimum* (Taylor, 1962), have traditionally been recognized in the northern and northeastern parts of Thailand, respectively (Taylor, 1962), although the latter species is now generally treated as a synonym of the former (Dubois, 1983, but see Discussion). The occurrence of congeners in the more southern region of the country, though briefly referred to by Chan-ard (2003), is not well documented.

During our field survey in Thailand, I collected many *Leptolalax* specimens, mainly along the western border of the country. Specimens from the northern region were tentatively identified as *L. pelodytoides* on the basis of examination of its types. They were basically similar in acoustic characteristics (Matsui, unpublished data). In contrast, specimens collected from more southern regions had calls that sound quite different from the northern *L. pelodytoides* to the human ear. Detailed analyses of acoustic and morphological characters have proved that there are three distinct forms that are different from *L. pelodytoides*. In this paper, I describe these three species as new to science.

MATERIALS AND METHODS

I collected *Leptolalax* or ascertained its occurrence without collection in northeastern (Loei Province), northern (Mae Hong Son and Chiang Mai Provinces), southwestern (Kanchanaburi and Prachuap Khiri Khan Provinces), and southern (Surat Thani and Narathiwat provinces) Thailand during my field surveys in various localities of this country between 1994 and 2004 (regional divisions following Nabhitabhata *et al.*, 2000). I failed to find specimens of this genus in other parts of Thailand.

I made recordings of calls in the field using a cassette tape recorder (Sony TC-D5) with an external microphone (Sony ECM-23). At the time of recording, I made temperature measurements using a quick-recording thermistor thermometer (Takara A 600). I analyzed the recorded calls using the computer programs SoundEdit Vers. 2 or SoundEdit Pro (MacroMind-Paracomp, Inc.) on a Macintosh computer. Methods of analyses are as described elsewhere (Matsui, 1997).

After recording calls, I collected specimens, took tissues for subsequent biochemical analysis, and fixed the specimens for vouchers. Specimens, fixed in 10% formalin and later preserved in 70% ethanol, are stored at the Chulalongkorn University Zoological Museum (CUZM) and the Graduate School of Human and Environmental Studies, Kyoto University (KUHE). Sixteen body measurements were taken, mainly following Matsui (1984, 1997): 1) snout-vent length (SVL); 2) head length (HL); 3) snout length (SL); 4) eye length (EL, including eyelid); 5) tympanum-eye length (T-EL); 6) tympanum diameter (TD); 7) head width (HW); 8) internarial distance (IND); 9) interorbital distance (IOD); 10) upper eyelid width (UEW); 11) lower arm length (LAL); 12) inner palmar tubercle length (IPTL); 13) tibia length (TL); 14) foot length (FL); 15) hindlimb length (HLL); 16) inner metatarsal tubercle length (IMTL). I made all measurements to the nearest 0.1 mm with dial calipers under a binocular dissecting microscope. The system of description of toe-webbing states follows that used by Savage (1975).

For comparisons, I examined specimens of *Leptolalax* stored at the Field Museum of Natural History, Chicago (FMNH); KUHE; Museo Civico di Storia Naturale, Genova (MSNG); Museum National d'Histoire Naturelle, Paris (MNHN); Natural History Museum, London (BM); Sabah Parks, Kota Kinabalu (SP); Universiti Malaysia Sabah, Kota Kinabalu (BORNEENSIS collection of UMS); Zoologisches Museum, Universität Humboldt, Berlin (ZMB);

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and Institut Royal des Sciences Naturelles de Belgique (IRSNB) (see Appendix 1).

SYSTEMATICS

Leptolalax melanoleucus sp. nov.
(Fig. 1A, B)

Diagnosis

A medium-sized form of the genus *Leptolalax*; male 26.6–28.8 mm (n=13), female 32.7 mm (n=1) SVL; tibiotarsal articulation usually reaching between eye and nostril; similar to *L. pelodytoides*, but with much lower dominant frequency of advertisement call of 3050 to 3200 Hz; differing from all congeners by unique ventral coloration, with large black markings on a white background.

Etymology

The specific epithet is from Greek meaning black and white, in reference to the contrasting ventral marking of the new species.

Holotype

KUHE 19720, an adult male from Khlong Saeng Wildlife Sanctuary, Surat Thani Province, Thailand (9° 15' N, 98° 39' E), collected on 29 August 1995 by Masafumi Matsui.

Paratypes

CUZM (A) 5270–5272; KUHE 19694, 19724, 19732 (six males); all collected between 28 and 29 August 1995 from the same locality as the holotype by Masafumi Matsui and Hidetoshi Ota.

Referred specimens

CUZM (A) 5273, 5274, KUHE 23820, 23844 (four males), 23845 (one female) from Khao Sok National Park, Surat Thani Province, Thailand (9° 00' N, 98° 38' E), collected 19–20 August 1997 by Masafumi Matsui; KUHE 35081 (one male) from Pilok, Thong Pha Pum, Kanchanaburi Province, Thailand (14° 49' N, 98° 31' E), collected on 3 January 2002 by Masafumi Matsui and Wichase Khonsue; IRSNB-KBIN 13243 (one male) from Klong Hat Som Pen, Muang, Ranong Province, Thailand (9° 57' N, 98° 41' E), collected on 1 September 2003 by O. S. G. Pauwels, C. Chimsunchart, and M. Sumontha.

Description of holotype (measurements in mm)

SVL 28.6; habitus moderately stocky; head longer (11.3) than broad (10.2); snout rounded, truncate in profile, projecting slightly beyond lower jaw; eye diameter (4.4) slightly greater than snout length (4.1); canthus distinct, slightly constricted; lore slightly oblique, slightly concave; nostril lateral, below canthus, distinctly closer to tip of snout than to eye; internarial distance (2.7) narrower than interorbital distance (3.3), latter subequal to upper eyelid (3.3); pineal spot absent; tympanum distinct, diameter (2.1) about half that of eye, and separated from eye by one-third of tympanic diameter (0.8); vomerine teeth absent; tongue notched, without papillae; a median, subgular vocal sac in the mid-ventral line; vocal openings posterior to rictus, close to eustachian tube openings.

Forelimb slender; fingers slender, unwebbed, first finger slightly shorter than second, latter slightly shorter than

fourth; tips slightly swollen; inner palmar tubercle large (1.4), not extending onto first metacarpal and smaller outer palmar tubercle; subarticular tubercles indistinct, replaced by indistinct callous tissue; nuptial pads absent.

Hindlimb relatively long (45.5); tibia relatively long (14.0), heels slightly overlapping when limbs are held at right angles to body; tibiotarsal articulation of adpressed limb reaching between eye and nostril; foot (12.3) shorter than tibia; third toe longer than fifth; toe tips similar to those of fingers; webbing confined to bases of toes (Fig. 2A), formula: I $1\frac{2}{3}$ –2+ II $1\frac{4}{5}$ –3 III $2\frac{2}{3}$ – $3\frac{4}{5}$ IV 4– $2\frac{2}{3}$ V; toes without lateral fringes; subarticular tubercles obscure, but elongate, replaced by low keratinous dermal ridges, a relatively short one on each of second, third, and fifth toes, larger ones on fourth toe; inner metatarsal tubercle low, length (1.0) less than half of first toe; no outer metatarsal tubercle.

Skin nearly smooth, scattered with small tubercles of varying sizes above; eyelid and top of snout without tubercles; a low, supratympanic ridge from eye to above axilla; sides with larger tubercles; chest and abdomen smooth; small, weak pectoral gland, femoral gland indistinct; a small, round, white gland above axilla; large glands anterior to sides of vent; ventrolateral glandular ridges indistinct; skin of gular region not modified.

Color in life

Olive brown dorsally on head and body, with indistinct dark brown markings, including interorbital one; tympanum masked black; no spot on canthus; lips barred with black; sides with small dark spots; groin with dark spot extending onto anterior half of thigh; large glands anterior to sides of vent white; limbs marked dorsally with alternating olive and dark brown crossbars; dark bar restricted to posterior side around the elbow, between upper and lower arms; sides of tibia with black spots, continuous as bars across dorsal surface; chin and throat white with dark brown vermiform lines; chest and abdomen white mottled with large, continuous black markings; ventral and posterior surfaces of thigh dark brown with few white spots; iris orange on upper half, silver reticulated with black on lower half.

Color in preservative

In preservative, color and pattern have not obviously changed, though they have generally faded. The dorsal coloration has slightly faded to grey-brown, and upper and lower halves of iris have become indistinguishable.

Eggs

The single female from Khao Sok released part of her eggs in a plastic container soon after collection. The diameter of 10 ova ranged from 1.38–1.57 (mean \pm 2SE=1.51 \pm 0.03) mm. Both animal and vegetal poles were uniformly cream in color.

Call characteristics

Calls were recorded at Khlong Saeng on 29 August 1995 at a ground temperature of 23.9°C. They consisted of a long series of notes, each composed of three to four indistinct pulses and lasting 40–63 ms (Fig. 3A). During active calling, the note-gap and note-repetition rates varied greatly, but were mostly 102–180 ms and about 6.1 per s, respec-

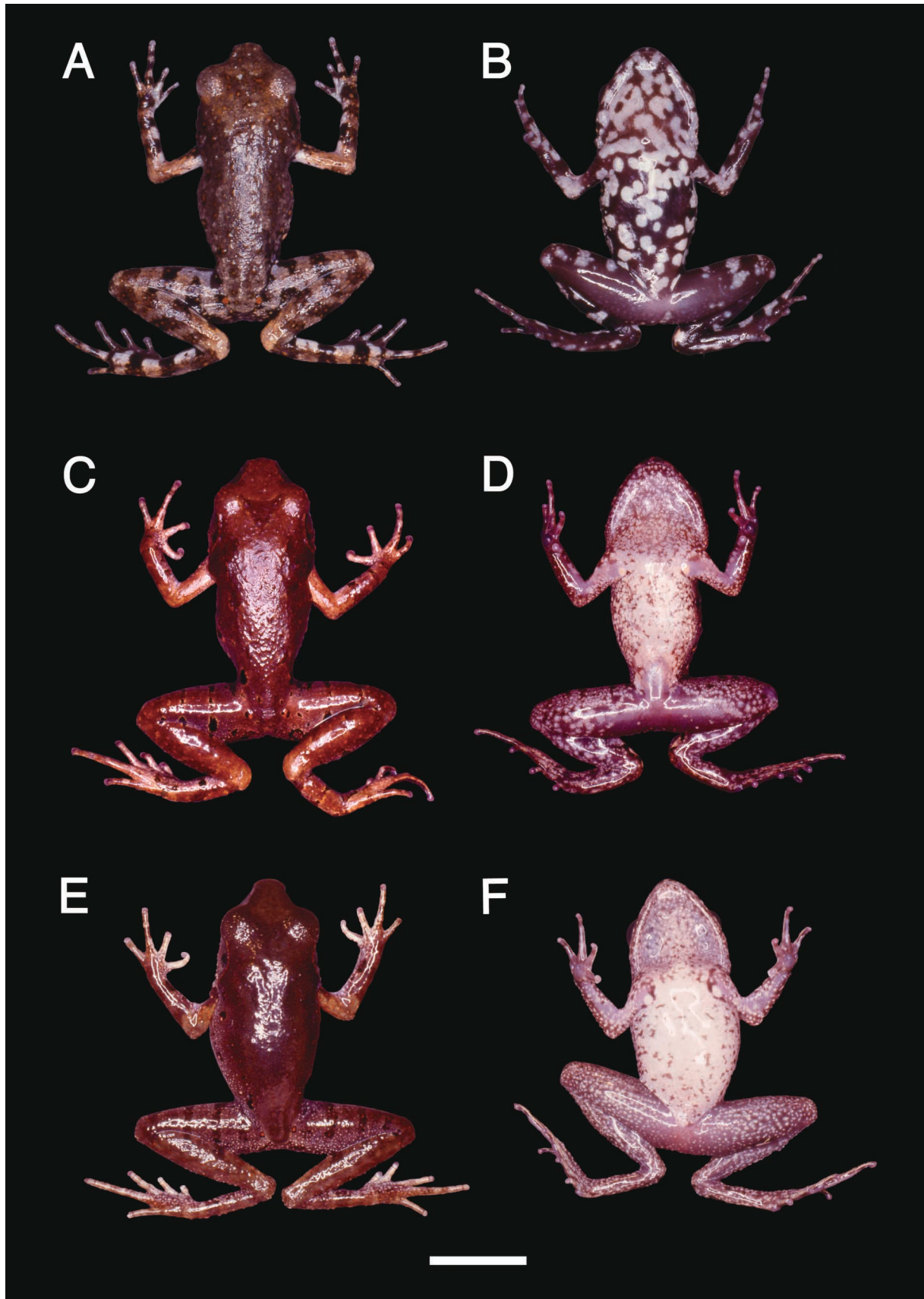


Fig. 1. Male holotypes of (A, B) *Leptolax melanoleucus* (KUHE 19720), (C, D) *L. fuliginosus* (KUHE 20174), and (E, F) *L. solus* (KUHE 23261); dorsal (A, C, E) and ventral views (B, D, F). Scale bar=10 mm.

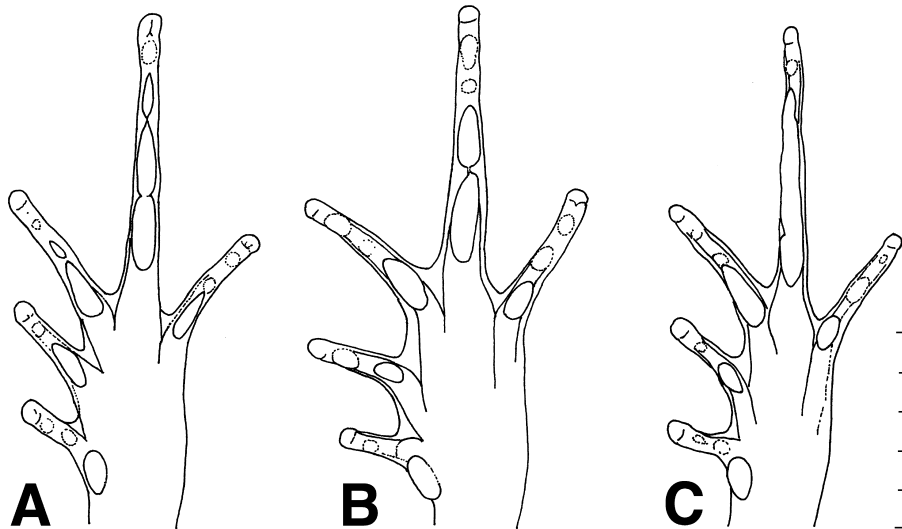


Fig. 2. Left feet of holotypes of (A) *Leptolax melanoleucus*, (B) *L. fuliginosus*, and (C) *L. solus*; ventral views. Scale bar=5 mm.

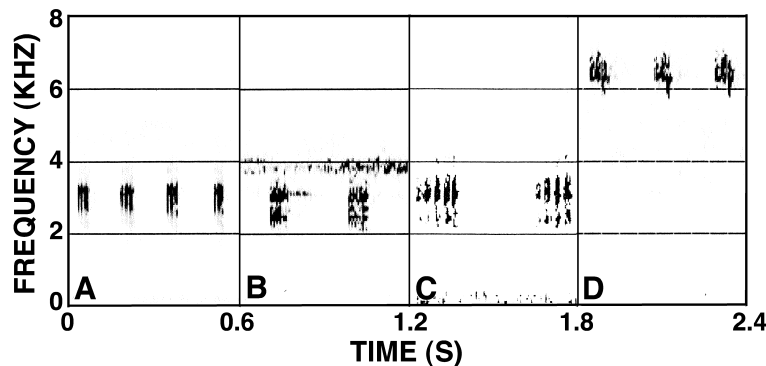


Fig. 3. Sonagrams of advertisement calls of (A) *Leptolax melanoleucus* from Khlong Saeng, Surat Thani, (B) *L. fuliginosus* from Pa Lao U, Prachuap Khiri Khan, (C) *L. solus* from Hala Bala, Narathiwat, and (D) *L. pelodytoides* from Doi Suthep, Chiang Mai.

tively. The dominant frequency was 3050–3300 hz, although the band spread over the 2600–3600 hz range. Harmonics were not evident, and frequency and intensity modulations were absent.

Calls recorded at Khao Sok on 19 August 1997 at air temperatures of 24.2–24.3°C consisted of one to three notes, each composed of four to eight indistinct pulse groups and lasting 130–260 ms, with a note gap of 220–290 ms. The note repetition rate was 2.1–2.3 per s, and the dominant frequency was 3100–3200 hz, although the band spread over the range of 2000–4000 hz. Harmonics were unclear, and both frequency and intensity modulation were absent.

Variation

Individuals of the type series are generally similar in morphology, and vary only slightly. Eye diameter is subequal to snout length in one individual and interorbital distance is slightly greater than upper eyelid width in four individuals. Tibiotarsal articulation of adpressed limb reaches the anterior corner of eye in three individuals. Males from Khlong Saeng and Khao Sok did not differ in SVL or any dimension relative to SVL (Dunn's multiple comparisons

test, $P > 0.05$). Some individuals have an elongated white oval spot on the rear surface of thigh at distal one-third.

The temporal characteristics of the call differ between the Khlong Saeng and Khao Sok populations, although the frequency characteristics are similar between them (see above).

Range

Southern part of the southwestern region to northern part of the southern region of Thailand. Besides the type locality, Khlong Saeng Wildlife Sanctuary, Surat Thani Province, the species was recorded from Muang, Ranong Province; Khao Sok National Park, Surat Thani Province; and Pilok, Thong Pha Pum, Kanchanaburi Province.

Natural History

At both Khlong Saeng and Khao Sok, males were calling at night on the ground among dead leaves and stones, on slopes 1–10 m from small streams (width < 2 m). Late August seems to be within the breeding season, as evidenced by a female releasing eggs on the night of collection at Khao Sok. In this female, no ova were left inside oviducts, but half-developed ova with a diameter of about 0.65 mm

were seen in ovaries. Therefore, multiple breeding with short intervals is expected. Associated species at Khlong Saeng were *Bufo parvus*, *Megophrys* sp., *Ingerana tasanae*, *Limnonectes blythi*, *L. doriae*, *L. kuhlii*, *Rana erythraea* and *R. nigrovittata*, and those at Khao Sok were *Bufo melanostictus*, *I. tasanae*, *Megophrys* sp., *Occidozyga* sp., *L. doriae*, *L. kuhlii*, and *R. erythraea*. At Pilok, no calls were heard in early January, probably because it was very cool. A single individual was found among stones on the bank of a nearly dried small stream (width < 2 m).

Leptolalax fuliginosus sp. nov.
(Fig. 1C, D)

Diagnosis

A medium-sized form of the genus *Leptolalax*; male 28.2–30.0 mm SVL (n=4); tibiotarsal articulation reaching anterior corner of eye; similar to *L. pelodytoides*, but with much lower dominant frequency of advertisement call of 2250 to 2430 Hz and dusty ventral side of head and body; similar to *L. melanoleucus* in body shape, but with relatively shorter head, smaller eye and tympanum, and larger inner metatarsal tubercle.

Etymology

The specific epithet is a Latin word meaning dusty, in reference to the ventral color of the new species as compared to that of *L. pelodytoides*.

Holotype

KUHE 20174, an adult male from Pa Lao U, Prachuap Khiri Khan Province, Thailand (12°32' N, 99°34' E), collected on 13 December 1995 by Masafumi Matsui and Kunio Araya.

Paratypes

CUZM (A) 5275, 5276; KUHE 20197 (three males); same data as the holotype.

Description of holotype (measurements in mm)

SVL 28.4; habitus moderately slender; head longer (10.7) than broad (9.8); snout rounded, rounded in profile, projecting beyond lower jaw; eye diameter (3.8) slightly smaller than snout length (4.2); canthus distinct, very slightly constricted; lore oblique, slightly concave; nostril lateral, below canthus, distinctly closer to tip of snout than to eye; internarial distance (2.8) narrower than interorbital distance (3.2), latter wider than upper eyelid (2.8); pineal spot absent; tympanum visible, diameter (1.6) less than half that of eye, and separated from eye by two-thirds of tympanic diameter (1.1); vomerine teeth absent; tongue notched, without papillae; a median, subgular vocal sac in the mid-ventral line; vocal openings posterior to rictus, close to eustachian tube openings.

Forelimb slender; fingers slender, unwebbed, first finger slightly shorter than second, latter slightly shorter than fourth; tips slightly swollen; inner palmar tubercle large (1.9), not extending onto first metacarpal and smaller outer palmar tubercle; subarticular tubercles indistinct, replaced by very low callous tissue; nuptial pads absent.

Hindlimb moderately long (45.2); tibia relatively long (13.7), heels overlapping when limbs are held at right angles

to body; tibiotarsal articulation of adpressed limb reaching anterior corner of eye; foot (13.2) slightly shorter than tibia; third toe longer than fifth; toe tips similar to those of fingers; webbing confined to bases of toes (Fig. 2B), formula: I $1\frac{4}{5}$ – $1\frac{3}{4}$ II $1\frac{2}{3}$ – $2\frac{1}{2}$ III $2\frac{1}{2}$ – $3\frac{3}{4}$ IV 4 – $2\frac{2}{3}$ V; toes weakly fringed laterally on the first three and base of fourth and fifth toes; subarticular tubercles obscure, but elongate, replaced by low keratinous dermal ridges, a relatively short one on each of second and fifth toes, larger ones on third and fourth toes; inner metatarsal tubercle low, length (1.7) about half of first toe; no outer metatarsal tubercle.

Skin nearly smooth, with a few tubercles of varying sizes above; a low, supratympanic ridge from eye to axilla; sides same as dorsum; chest and abdomen smooth; weak, but large pectoral and weak femoral glands; a small, round, white gland just above axilla; ventrolateral glandular ridges incomplete; skin of gular region not modified.

Color in life

Light brown dorsally on head and body, scattered with faint dark spots, including a dark, reverse-triangle interorbital spot; posterior half of tympanum masked black; black band below canthus; lips barred with black; sides with several large, dark spots; groin with dark spot not extending onto thigh; limbs marked dorsally with narrow dark brown crossbars, especially narrow on hindlimb; elbow and upper arm without bar dorsally; sides of tibia with black spots, not continuous as bars across dorsal surface; posterior side of thigh dusky, becoming gradually darker toward the rear surface, which is quite dark; an elongated white oval spot on the rear surface of thigh at distal one-third; throat dusky; chest and abdomen white, dusted with fine brown network laterally; ventral surfaces of legs dusky, dotted with light brown; iris reddish orange in upper half, golden reticulated with black in lower half.

Color in preservative

In preservative, the dorsal coloration has slightly faded to olive brown. Otherwise no obvious changes in color or pattern have occurred. However, eye color has faded and upper and lower halves of iris have become indistinguishable.

Call characteristics

Calls recorded on 13 December 1995 at air and ground temperatures of 19.3 and 19.6°C, respectively, consisted of a long series of notes, each composed of six to nine indistinct pulses and lasting 51–80 ms (Fig. 3B). The note-gap and the note-repetition rates varied greatly, 188–402 ms and 2.9 per s, respectively. The frequency range spread over 2060–2810 Hz, with the dominant being 2250–2430 Hz. Harmonics were unclear, and frequency and intensity modulations were lacking.

Variation

Individuals of the type series are generally uniform in morphology. In some individuals, eye diameter and snout length are subequal, as are internarial and interorbital distances, and interorbital distance and upper eyelid width, respectively.

Range

Known only from the type locality, Pa Lao U, Prachuap Khiri Khan Province, southern part of southwestern Thailand

Natural History

In mid-December, males were calling at night among stones and litter on the floor of a forest along a stream (width > 5 m). Associated species observed were *Bufo asper*, *Amolops panhai*, *Rana livida*, *R. nigrovittata*, and *Taylorana hascheana*.

Leptolalax solus **sp. nov.**
(Fig. 1E, F)

Diagnosis

A medium-sized form of the genus *Leptolalax*, male 27.6 mm SVL ($n=1$); tibiotarsal articulation reaching nostril; more similar to *L. heteropus* than to *L. pelodytoides*, but differing from the former by relatively narrower head, longer hindlimb, and larger inner metatarsal tubercle, as well as by temporal pattern of advertisement call, with successive notes constant in duration.

Etymology

The specific epithet is a Latin word meaning single or lonely, alluding to the collection of only one male that began calling in captivity, where he could not attract a mate.

Holotype

KUHE 23261, an adult male from Bala in Hala Bala Wildlife Sanctuary, Narathiwat Province, Thailand (5° 49' N, 101° 47' E), collected on 10 January 1997 by Masafumi Matsui.

Description of holotype (measurements in mm)

SVL 27.6; habitus moderately slender; head longer (11.7) than broad (9.7); snout rounded, truncate in profile, projecting slightly beyond lower jaw; eye large, diameter (4.3) subequal to snout length (4.2); canthus distinct, straight; lore slightly oblique, slightly concave; nostril lateral, below canthus, distinctly closer to tip of snout than to eye; internarial distance (2.7) narrower than interorbital distance (2.9), latter narrower than upper eyelid (3.1); pineal spot absent; tympanum distinct, diameter (1.8) less than half that of eye, and separated from eye by one-half of tympanic diameter (1.0); vomerine teeth absent; tongue notched, with papillae; a median, subgular vocal sac in the mid-ventral line; vocal openings posterior to rictus, close to eustachian tube openings.

Forelimb slender; fingers slender, unwebbed, first and fourth fingers subequal and longer than second; tips slightly swollen; inner palmar tubercle very large (2.0), not extending onto first metacarpal; smaller outer palmar tubercle; subarticular tubercles indistinct, replaced by long, low callous tissue; nuptial pads absent.

Hindlimb long (47.0); tibia long (14.9), heels overlapping when limbs are held at right angles to body; tibiotarsal articulation of adpressed limb reaching nostril; foot much shorter (12.7) than tibia; third toe longer than fifth; toe tips similar to those of fingers; webbing confined to bases of toes (Fig. 2C), formula: I $1\frac{1}{2}$ –2+ II $1\frac{3}{4}$ –3+ III $2\frac{3}{4}$ –4 IV 4+– $2\frac{2}{3}$ V; toes with lateral fringes; subarticular tubercles obscure, but elongate,

replaced by large keratinous dermal ridges, a relatively short one on each of second and fifth toes, larger one on third toe, ridge covering entire underside of fourth toe except distal portion; inner metatarsal tubercle distinct, length (1.9) more than half of first toe; no outer metatarsal tubercle.

Skin weakly shagreened, scattered with small tubercles above; top of snout and head without tubercles; a conspicuous, supratympanic ridge from eye to axilla; sides scattered with larger tubercles; chest and abdomen smooth; small, weak pectoral gland and large, elongate femoral gland; no gland above axilla; ventrolateral glandular ridges absent; skin of gular region not modified.

Color in life

Chocolate-brown dorsally on head and body, with faint interorbital spot of dark brown; tympanum, except for annulus, and inside of supratympanic fold dark brown; dark spots below canthus and sides of snout tip; lips partially barred with dark brown; sides with dark brown flecks; groin without dark spot; limbs marked dorsally with alternating chocolate and dark brown crossbars, the darker ones much narrower; area around the elbow, between upper and lower arms, light brown without dark bars; sides of tibia with black spots, not continuous as bars across dorsal surface; an elongated white oval spot on the rear surface of thigh at distal one-third; throat dusky, dotted with dark brown; chest and abdomen white scattered with dark brown flecks; ventral surfaces of legs dusky, densely scattered with small white spots; iris dark red on upper half, dark brown on lower half.

Color in preservative

In preservative, the dorsal coloration has slightly faded to maroon. Otherwise no obvious changes in color or pattern have occurred, except for iris, the upper and lower halves of which have become indistinguishable.

Call characteristics

Calls recorded at air temperatures of 24.2–24.3°C (Fig. 3C) consisted of one to three notes. Each note was composed of four to eight indistinct pulse groups and lasted 130–260 ms. The note gap and note repetition rates were 220–290 ms and 2.1–2.3 per s, respectively. The frequency bands spread over the 2000–4000 Hz range, and the dominant was 3100–3200 Hz. Harmonics were not evident, and frequency modulation and intensity modulation were absent.

Range

Known only from the type locality, Bala in Hala Bala Wildlife Sanctuary, Narathiwat Province, southernmost Thailand near Malaysian border.

Natural History

The male holotype was collected at night among rocks 10 m apart from a large stream (width > 5 m) in a rainforest. No calls were heard in the field, but in captivity the male intermittently called from midnight to early morning. Associated species on the night of collection were *Bufo parvus*, *Amolops larutensis*, *Rana chalconota*, and *Limnonectes laticeps*.

Table 1. Measurements of 16 characters in species of *Leptolalax*. SVL ($\bar{X} \pm 1SD$, in mm) and medians of ratios (R) of other characters to SVL, followed by ranges in parenthesis. See text for character abbreviations.

Species	Locality	Sex	SVL	RHL	RHW	RIND	RIOD	RUEW
<i>L. melanoleucus</i>	Khlong Saeng	M	27.6 \pm 0.83	39.9	36.3	10.5	11.5	11.3
		(N=7)	(26.6–28.8)	(37.9–41.1)	(34.0–38.2)	(9.4–11.2)	(10.0–12.8)	(10.8–11.5)
	Khaosok	M	27.6 \pm 0.94	40.4	36.7	10.7	10.7	11.3
		(N=4)	(26.9–29.0)	(39.6–41.0)	(36.3–36.9)	(10.3–11.0)	(9.9–11.2)	(10.6–11.7)
	Khaosok	F	32.7	38.8	36.7	8.9	11.0	11.0
		(N=1)						
<i>L. fuliginosus</i>	Pa Lao U	M	28.9 \pm 0.81	38.6	36.1	10.3	10.7	10.1
		(N=4)	(28.2–30.0)	(37.7–39.3)	(34.4–38.0)	(9.0–11.0)	(10.0–11.3)	(9.9–11.0)
<i>L. solus</i>	Hala Bala	M	27.6	42.4	35.1	9.8	10.5	11.2
		(N=1)						
<i>L. pelodytoides</i>	Karen, Myanmar*	M	26.7	38.7	36.3	10.3	10.9	10.3
		(N=2)	(24.7–28.6)	(38.1–39.3)	(35.3–37.2)	(10.1–10.5)	(10.5–11.2)	(10.1–10.5)
Species	Locality	Sex	RSL	REL	RTD	RE-TL	RLAL	RIPTL
<i>L. melanoleucus</i>	Khlong Saeng	M	15.0	15.4	7.5	3.5	56.0	5.5
		(N=7)	(14.3–16.1)	(15.0–17.1)	(7.1–8.0)	(2.8–3.8)	(52.1–56.4)	(4.8–6.4)
	Khaosok	M	15.2	15.3	7.2	3.6	54.9	6.4
		(N=4)	(14.3–15.4)	(14.6–17.2)	(6.9–7.7)	(3.3–3.7)	(52.4–55.8)	(6.2–6.7)
	Khaosok	F	14.7	14.7	8.6	3.4	55.4	5.8
		(N=1)						
<i>L. fuliginosus</i>	Pa Lao U	M	15.0	13.6	6.0	3.9	53.7	6.1
		(N=4)	(14.3–15.6)	(13.4–14.7)	(5.6–6.6)	(3.5–4.1)	(52.3–54.5)	(6.0–6.7)
<i>L. solus</i>	Hala Bala	M	15.2	15.6	6.5	3.6	54.0	7.2
		(N=1)						
<i>L. pelodytoides</i>	Karen, Myanmar*	M	15.4	14.8	6.8	4.0	51.8	
		(N=2)		(13.8–15.8)	(6.6–6.9)		(51.0–52.6)	
Species	Locality	Sex	RTL	RFL	RHLL	RIMTL		
<i>L. melanoleucus</i>	Khlong Saeng	M	48.9	44.6	162.5	4.5		
		(N=7)	(45.8–51.1)	(39.9–45.1)	(151.7–169.2)	(4.2–5.4)		
	Khaosok	M	49.7	44.2	161.8	5.5		
		(N=4)	(48.0–51.3)	(44.0–45.7)	(158.6–166.9)	(5.2–6.2)		
	Khaosok	F	48.3	44.6	160.6	4.9		
		(N=1)						
<i>L. fuliginosus</i>	Pa Lao U	M	48.3	46.0	159.4	5.6		
		(N=4)	(46.7–50.4)	(44.7–48.6)	(153.7–177.2)	(5.3–6.0)		
<i>L. solus</i>	Hala Bala	M	54.0	46.0	170.3	6.9		
		(N=1)						
<i>L. pelodytoides</i>	Karen, Myanmar*	M	49.7	49.9	165.3	5.3		
		(N=2)	(49.7–49.8)	(49.4–50.3)	(165.0–165.6)			

*Specimens stored in MSNG and BM.

DISCUSSION

Acoustic comparisons

Because males of most anuran species utilize species-specific acoustic signals for attracting conspecific females, call characteristics play a large role in taxonomic studies (e.g., Matsui *et al.*, 1986; Matsui, 1997). In *L. melanoleucus* described here, the temporal characteristics of calls differed between two different populations, but the frequency characteristics were nearly the same. The two populations are treated herein as a single species because of their close morphological similarity, although the possibility is not rejected that the temporal differences observed between their calls actually indicate substantial genetic differentiation. In order to assess this, comparisons of the two populations by other methods such as biochemical ones are necessary. Among *Leptolalax* species, however, frequency properties

usually differ more than temporal ones (Matsui, 1997, unpublished).

All known Bornean members of *Leptolalax* for which calls have been reported [*L. arayai* Matsui, 1997; *L. dringi* Dubois, 1987; *L. gracilis* (Günther, 1872); *L. hamidi* Matsui, 1997; *L. pictus* Malkmus, 1992] markedly differ acoustically from the continental species, including the three new species (Matsui, 1997, unpublished; Malkmus *et al.*, 2002). The call of the remaining Bornean species, *L. maurus* Inger, Lakim, Biun, and Yambun, 1997, is unknown.

Among the three new species, *L. fuliginosus* superficially resembles *L. pelodytoides* (Boulenger, 1893) from China to northern Thailand. However, the dominant frequency in the calls of *L. pelodytoides* recorded at Doi Suthep, Chiang Mai, at an air temperature of 22.7 C spread over 6350–6550 Hz (Matsui, unpublished; Fig. 3D), and is thus drastically different from that of *L. fuliginosus*, as well

as of the other two new species (2250–3300 Hz). This difference is not attributable to differences in ambient temperature or body size. Similarly, *L. oshanensis* (Liu, 1950) from Sichuan and *L. liui* Fei and Ye in Fei, Ye, and Huang (1991) from Hong Kong, respectively 4000–5000 and 4500–5500 Hz in dominant frequency (Matsui, unpublished), are distinct from the three new species in this character.

Leptotalax solus superficially resembles *L. heteropus* (Boulenger, 1900) from the Malay Peninsula more than *L. pelodytoides*. As was shown by Matsui (1997), however, calls in *L. heteropus* consist of three notes whose lengths are not constant (vs. nearly constant in *L. solus*). Also, the first note lasts 80 ms, and the second and third notes are shorter, each lasting 28 ms in *L. heteropus*, whereas all notes last 130–260 ms in *L. solus*. The dominant frequency in calls of the former is 2833 Hz in the first note, but is slightly lower in subsequent notes (vs. 3100–3200 Hz in all notes in *L. solus*). Thus, the two species decidedly differ in acoustic characteristics.

Morphological comparisons

Leptotalax pelodytoides differs from the three new species not only in acoustic traits, but also in the completely or nearly immaculate venter and the better developed lateral fringes along the toes (Matsui's observation of type series). Likewise, *L. oshanensis* and *L. liui* have the ventral surface of the body unmarked or with only small, light gray spots (Fei, 1991; Matsui, unpublished data). Thus, they clearly differ from *L. melanoleucus*, which has a venter mottled with black and white. *Leptotalax fuliginosus* resembles some individuals of *L. oshanensis* and *L. liui* in having a dusty venter. However, *L. fuliginosus* differs from *L. oshanensis* in having webbing among the toes [nearly lacking in *L. oshanensis* (Inger *et al.*, 1990)], and from *L. liui* in having a slightly larger body [male SVL=28.2–30.0 mm, as compared to 23–28.7 mm in *L. liui* (Fei *et al.*, 1991)] and lacking the wide lateral fringe on the toes [present in *L. liui* (Fei *et al.*, 1991)].

Leptotalax solus superficially resembles *L. heteropus*, but differs from it in details of morphology; males of topotypic *L. heteropus* have SVL 24.6–26.0 mm (vs. 27.6 mm in *L. solus*), HW 36–41% (vs. 35%), TL 50–53% (vs. 54%), FL 40–46% (vs. 46%), and IMTL 3.6–4.4% (vs. 6.9%), all relative to SVL (Matsui, unpublished). Although Berry (1975) gave larger SVL (33–35 mm) for *L. heteropus*, she did not refer to the sex, and the values may have included females.

Of the species for which acoustic information is lacking, Bornean *L. maurus* has a unique dark venter (Inger *et al.*, 1997; Malkmus *et al.*, 2002), and is thus distinct from the three new species. Of the continental species, *L. tuberosus* Inger, Orlov, and Darevsky, 1999 from Vietnam lacks a clearly visible tympanum (Matsui's own observation of type series), unlike all other congeners, including the three new species.

The following species are distinctly larger than the three new species (SVL=26.6–30.0 mm in males): *L. bourreti* Dubois, 1983 (SVL=29.3–36.2 mm in males; Matsui's own observations), *L. sungi* Lathrop, Murphy, Orlov, and Ho, 1998 (SVL=48.3–52.7 mm in males; Lathrop *et al.*, 1998), and *L. nahangensis* Lathrop, Murphy, Orlov, and Ho, 1998 (SVL=40.8 mm in unique male holotype; Lathrop *et al.*, 1998), all from Vietnam; and *L. kajangensis* Grismer, Gris-

mer, and Youmans, 2004 from Malaysia (SVL=34.0–35.0 mm in males). In contrast, *L. pluvialis* Ohler, Marquis, Swan, and Grosjean, 2000 from Vietnam is much smaller than the three new species (male SVL=21.3–22.3 mm; Ohler *et al.*, 2000). Of these, *L. sungi*, *L. nahangensis*, and *L. kajangensis* have the ventral surface of body unspotted or only with small, light gray spots (Lathrop *et al.*, 1998; Grismer *et al.*, 2004), and *L. pluvialis* has a gray ventrum with dark gray marbling (Matsui's own observation of the type series). Thus, they are more similar to *L. fuliginosus* and *L. solus* than to *L. melanoleucus* (see comments in the first paragraph of this subsection). However, all of them are quite different from the three new species in body size, as noted above. In addition, *L. pluvialis* lacks toe webbing, unlike the three new species. Although *L. bourreti* slightly overlaps in body size, it has no marking on the ventrum, unlike the three new species.

Two Chinese species are reported to have a maculate venter like *L. melanoleucus*, and unlike *L. fuliginosus* or *L. solus*. In *L. alpinus* Fei, Ye, and Huang, 1991, the venter is more or less dark spotted, but the distribution of dark markings is much more limited than in *L. melanoleucus*, judging from Fig. 33 in Plate VI of Fei *et al.* (2005). Additionally, *L. alpinus* is slightly smaller in male body size (male SVL=24.0–26.4 mm; Fei *et al.*, 1991) than the three new species. *Leptotalax ventripunctatus* Fei, Ye, and Li in Fei, Ye, and Huang (1991) also resembles *L. melanoleucus* both in body size (male SVL about 26.5 mm; Fei, 1999) and the presence of clear, dark markings ventrally (Fei, 1991). However, the pattern of dark markings in *L. ventripunctatus* is again quite different from that of *L. melanoleucus*: in *L. ventripunctatus*, the dark area is restricted to the chest and abdomen, not extending to the throat (see Fig. 31 in Plate VI of Fei *et al.*, 2005). Furthermore, *L. ventripunctatus* has longitudinal skin ridges on the dorsum (Fei, 1999).

Taxonomic diversity and biogeography

In a recent publication on the amphibian fauna of Thailand, Chan-ard (2003) listed four species of *Leptotalax* (*L. bourreti*, *L. gracilis*, *L. heteropus*, and *L. pelodytoides*) from this country. However, because this work is an illustrated guidebook, sources of data or the bases for identification are not provided.

As noted in the Introduction, another species, *L. minimum*, is described from Doi Suthep (Taylor, 1962). Dubois (1981), however, synonymized this species with Chinese *L. oshanensis*, and the latter with *L. pelodytoides* (Dubois, 1983). Although Inger *et al.* (1990) retained *L. oshanensis* as valid, they regarded it as a subspecies of *L. pelodytoides* and considered its range as restricted to southwestern China. Thus, the exact status of *L. minimum* is unclear, and the name is now subsumed under the name *L. pelodytoides*.

Leptotalax pelodytoides (including *L. minimum*) is currently believed to occur in a very wide range from Myanmar (Boulenger, 1893) through Thailand (Taylor, 1962) and Vietnam (Inger *et al.*, 1999) to southern China (Fei *et al.*, 2005), and actually exhibits geographical variation even within Thailand (Matsui, unpublished data). Chan-ard (2003) listed *L. bourreti* from the distributional range of *L. pelodytoides*, but the species identification is dubious (see above). His action may also be related to the complex nature of *L. pel-*

odytoides and, thus, further work is needed on this species. Even so, the acoustic characteristics of Thai populations of *L. pelodytoides* are basically similar, and are quite distinct from those of the three new species, as discussed above.

Leptolax solus is geographically and morphologically close to *L. heteropus*. An individual of *L. heteropus* shown by Chan-ard (2003) in a photograph undoubtedly looks more like *L. heteropus* than *L. solus*, and the body size given therein (33–35 mm) is larger than that of *L. solus*. However, the origin of the individual photographed is unclear, and the body size coincides with that given by Berry (1975). Thus, the form from Thailand identified as *L. heteropus* by Chan-ard (2003), if it exists, may actually represent *L. solus*. Similarly, from the map in Chan-ard (2003), *L. gracilis* (not illustrated in a photograph) may actually be *L. melanoleucus*, because the body size documented (32–51 mm) again completely matches that of *L. gracilis* given by Berry (1975). In my opinion, *L. gracilis* is endemic to Borneo, and records from the Malay Peninsula (Berry, 1975; Grandison, 1972) may represent another, undescribed species.

The pattern of distribution within Thailand of the three new species, together with that of *L. pelodytoides*, is interesting (Fig. 4). Along the Myanmar border, *L. pelodytoides* extends from the northern and northeastern regions southward to Erawan, Kanchanaburi. The known distributional range of *L. melanoleucus* is disjunct, with its northern limit (Pilok, Kanchanaburi) extending slightly northward of the southern limit of *L. pelodytoides*. The southern range of *L. melanoleucus* in Muang (Ranong) and in Khlong Saeng and Khao Sok (Surat Thani) extends slightly south of the Isthmus of Kra. Between these two ranges of *L. melanoleucus*, *L. fuliginosus* occurs in Pa Lao U (Prachuap Khiri Khan), as if displacing northern *L. pelodytoides*. In the south of Surat Thani, *L. solus* occurs in the extreme south of Hala Bala, Narathiwat. No *Leptolax* species has been found in between.

To date, no sympatric occurrence of two or more species of the genus has ever been detected, but the southern limit of *L. pelodytoides* and the northern limit of *L. melanoleucus* are not distant. These two species have different calls and could co-occur through pre-mating reproductive isolation. Thus, their sympatric occurrence is not unexpected. A ranid, *Amolops panhai*, has a range similar to that of *L. melanoleucus* (Pilok and Ranong), and like *L. fuliginosus* is also found in Pa Lao U (Matsui and Nabhitabhata, 2006). Therefore, it is also possible that *L. melanoleucus* has a more continuous range, overlapping the range of *L. fuliginosus*. Because these species have similar calls, at least to human ear, whether or not they can co-exist is an interesting problem.

This complicated pattern of distribution should be more accurately documented by adding locality records of correctly identified specimens. Further field surveys in Thailand, Myanmar, and Malaysia, as well as re-examination of specimens on which the records of each species were based by previous authors, are badly needed in order to understand pattern of distribution and to infer the evolutionary history of the genus. Even so, the discovery of two of the three new species (*L. melanoleucus* and *L. fuliginosus*) provides another example of occurrence of distinct species of congeners between northern and southern regions around

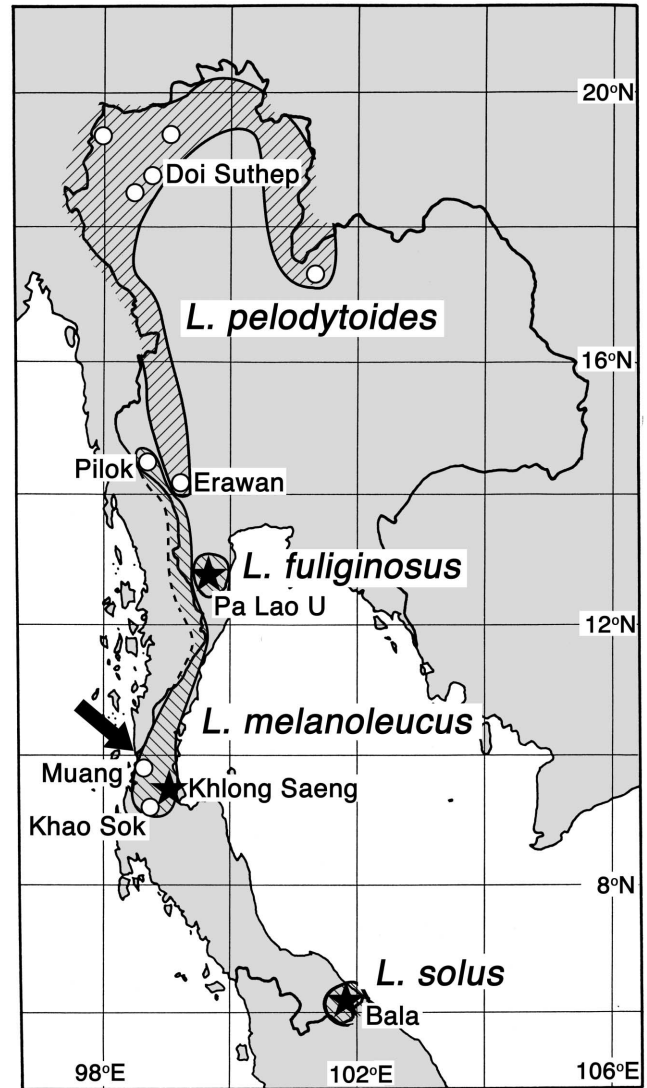


Fig. 4. Map of Thailand showing the known distributions of four species of *Leptolax* (open circles) and the type localities of the three new species (closed stars). Black arrow indicates the Isthmus of Kra.

the Isthmus of Kra, the base of peninsular Thailand (*Ansonia kraensis*: Matsui *et al.*, 2005; *Amolops panhai*: Matsui and Nabhitabhata, 2006).

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Appendix 1. Specimens of *Leptolalax* examined for comparisons. For museum acronyms, see text.

L. arayai Matsui, 1997: SP 01804 (holotype), BORNEENSIS 22623, 22624, 22692, 22693, 22739-22747, 22783 (topotypes), 22903, 22931; *L. bourreti* Dubois, 1983: MNHN 1938.0094 (holotype), 1938.0093, 1938.0095 (paratypes), 1999.5665, 1999.5667-1999.5669, 1999.5671-1999.5673; *L. dringi* Dubois, 1987: BORNEENSIS 22681-22691, 22701, 22748, 22749, 22756, 22760, 22784-22786, 22980, 23029, 23034, 23482; *L. gracilis* (Günther, 1872): BM 1944.2.25.5 (=92.2.19.35, holotype), KUHE 10634-10637, 10717, 12019, 12020, 12023 (topotypes), 17133, 17136, 17168, 17183, 17273, 17283, 17665; *L. hamidi* Matsui, 1997: KUHE 17546 (holotype), 17374, 17545 (paratypes); *L. heteropus* (Boulenger, 1900): KUHE 15432, 15433, 15485-15490 (topotypes); *L. liui* Fei and Ye In Fei, Ye, and Huang, 1991: KUHE 21705; *L. minimum* Taylor, 1962: FMNH 178229 (paratype); *L. maurus* Inger, Lakim, Biun, and Yambun, 1997: SP 2531 (holotype); *L. pelodytoides* (Boulenger, 1893): MSNG CE 29845A (lectotype), 29845B (paralectotype), BM 1947.2.25.14 (=93.10.9.46, paralectotype), ZMB 11588, KUHE 19113, 19130-19134, 19200, 19201, 19210, 19220-19224, 19229-19231, 19249, 19250, 19255-19262, 19809, 19815, 19816, 19993-19998, 20004-20016, 20024-20027, 20039-20043, 23733; *L. pictus* Malkmus, 1992: BORNEENSIS 22837-22839, 22859, 22864, 22894 (topotypes), 8871-8876, 12422, 12426, 12602, 12635, 12697, 22350, 22351, 22967, 22995, 23050, 23303, 23304, 23308, 23317, 23483, 23484, 23495-23498; *L. pluvialis* Ohler, Marquis, Swan, and Grosjean, 2000: MNHN 1999.5675 (holotype), 1999.5674, 1999.5676 (paratypes); *L. tuberosus* Inger, Orlov, and Darevsky, 1999: FMNH 252846, 252851, 252854, 252856, 252859 (paratypes).